



Taxonomy, biology, and efficacy of two Australian parasitoids of the eucalyptus gall wasp, *Leptocybe invasa* Fisher & La Salle (Hymenoptera: Eulophidae: Tetrastichinae)

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Abstract

Two species of Tetrastichinae (Hymenoptera: Eulophidae) from Australia are described as parasitoids of *Leptocybe invasa* Fisher & La Salle: *Quadrastichus mendeli* Kim & La Salle sp.nov. and *Selitrichodes kryceri* Kim & La Salle sp. nov. These parasitoids were introduced to Israel as part of a biological control program to counter the severe levels of damage caused by *L. invasa* to *Eucalyptus* plantations throughout the Mediterranean Basin. The biology of these species, as well as their potential as biological control agents, is discussed. Both species are now successfully established in Israel. The parasitoids were collected from *L. invasa* galls on 3–4 year old *Eucalyptus tereticornis* trees in central west Queensland, between Gympie and Hervey Bay, and on the Atherton Tableland. Both species are small (about 1 mm in length), solitary, and apparently ectoparasitic wasps. *S. kryceri* is biparental whereas *Q. mendeli* is uniparental. Maximum survival (~ 6 days at 25°C) for both species was obtained when they were fed with honey solution. *S. kryceri* and *Q. mendeli* successfully parasitized approximately 2.2 and 2.5 gall units per day, respectively. Both species developed on both young and mature host larvae. *L. invasa* may be considered as an early colonizer of regenerated young stands in Australia, which may imply that its parasitoids will display a similar fast-tracking behavior with respect to their host in its invasive range. The generic status of *Selitrichodes* is reinstated, with *Epomphaloides* and *Zagrammosomoides* placed as new synonyms of *Selitrichodes*.

Key words: Hymenoptera, Eulophidae, Selitrichodes, Quadrastichus, gall inducer, parasitoids, Eucalyptus

Introduction

Within the last decade, the invasive eucalyptus gall wasp, *Leptocybe invasa* Fisher & La Salle (Hymenoptera: Eulophidae) became established in the Mediterranean Basin (Arzone & Alma 2000; Viggiani *et al.* 2000; Aytar 2003; Mendel *et al.* 2004; Pujade-Villar & Riba-Flinch 2004; Ramadan 2004; Doğanlar 2005), and subsequently spread to SubSaharan Africa, India and Southeast Asia (CABI 2007) and quite recently Brazil (V.A. Costa, E. Berti-Filho, J.L. Stape, pers. comm., 2008). The gall inducer develops successfully on eucalyptus species of the section Exsertaria, among which *Eucalyptus camaldulensis* is particularly susceptible. *E. camaldulensis* is one of the best known eucalyptus trees outside Australia and economically is the most important hardwood species of the dry lowland areas in the entire Mediterranean and Middle East regions (FAO 1979). The wasp forms typical galls in the form of distinct swellings on the leaf midribs, petioles and stems on new foliage on trees of all ages, including nursery stock. Heavy galling causes the leaves to warp and in extreme cases it may stunt the growth of the tree (e.g., Mendel *et al.* 2004). Because of the severe damage caused by *L. invasa* to eucalyptus plantations worldwide, a search for its natural enemies was initiated in 2003.

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There have been two previous documented cases of classical biological control against gall inducing wasps. The first project was directed against the chestnut gall wasp, *Dryocosmus kuriphilus* Yasumatsu (Hymenoptera: Cynipidae), which was successfully controlled by *Torymus sinensis* Kamijo (Hymenoptera: Torymidae), which was introduced from China to Japan for that purpose (Moriya *et al.* 2003). The second project is currently being conducted against the eucalyptus gall wasp *Ophelimus maskelli* (Ashmead) (Hymenoptera: Eulophidae) (Mendel *et al.* 2007; Protasov *et al.* 2007a, b), and it appears to that complete control of this pest will be achieved.

Classical biological control has long been a principal tool in the efforts to minimize the adverse effects of invasive arthropods, and the present study is a part of the effort to discover the parasitoids of *L. invasa* in its homeland. Australian populations of *L. invasa* were discovered in Queensland. Two families, represented by three genera of parasitoids, were dominant among those that emerged from *L. invasa*-induced galls collected in Australia. They were the Torymidae (two species of *Megastigmus*), and the Eulophidae (one species of *Selitrichodes* and one of *Quadrastichus*). The latter two species are addressed in the present study, and information is presented on the taxonomy and natural history of these eulophids and on their recovery from *L. invasa* populations in Israel.

To date, about 100 species of Chalcidoidea are known to be associated with galls on eucalypts (Noyes 2003). The most common group of Australian gall inducers on *Eucalyptus* are wasps in the family Eulophidae, and this family includes species which are gall inducers, parasitoids of gall inducers and inquilines (La Salle 2005). It is interesting that in the present paper, as in the case of another gall inducing wasp *Ophelimus maskelli* (Protasov *et al.* 2007a; Mendel *et al.* 2007), the family Eulophidae contains both the invasive pest and its principal biological control agents.

Natural history of Leptocybe invasa parasitoids

Surveyed areas

Three surveys were conducted in Australia to discover parasitoids of *L. invasa* and, in light of tests of host susceptibility conducted in Israel (Mendel *et al.* 2004), the surveys were focused on eucalyptus species of the section Exsertaria: *E. camaldulensis* Dehnh., *E. tereticornis* Smith and *E. rudis* Endl., as well as planted hybrids of the first two of these species with *E. globulus* Labill. and *E. grandis* W. Hill, which are also highly susceptible to the *L. invasa*.

All three expeditions searched for galls that resembled those induced by *L. invasa*. Trees were distinguished between young trees (up to 5–6 years after natural regeneration) growing in river beds or in plantations, and adult trees in natural stands along rivers or in experimental stands.

The first survey was carried out in October 2003 in two major areas: south-western Australia, south of Perth, concentrated mainly on natural stands and plantations of *E. rudis* (locations: Alcola, Anketell, Balingup, Bunbury, Ilfarcomba, Mundijong and Narrogin); south-eastern Australia (south of Sydney in NSW, and in northern Victoria) concentrated mainly on natural stands and plantations of *E. camaldulensis* and, to a lesser extent, on *E. tereticornis* and *E. grandis* (locations: Avenel, Barmah Forest, Deniliquin, Hume Wair (near Albury), Jingellic, Mt. Alfred, the Murrumbidgee River near Wagga Wagga, Shepperton, Talmalmo, Tatura, the Wonga Wetland and Yarrawonga).

The second survey was conducted in October–November 2004 and concentrated on natural stands and plantations on eight sites in the Taree area of north-eastern NSW, where it focused on *E. tereticornis*, planted stands of *E. grandis X E. camaldulensis*, and on a natural stand of *E. amplyfolia* Naudin (also a member of the section Exsertaria). This survey also covered the coastal areas of south-eastern Queensland, mainly along the Brisbane River and its tributaries, and small irrigated plantations in the Brisbane city area.

The third survey was conducted in April-May 2006 in two major areas in Queensland: plantations and

natural regeneration sites between Gympie and Hervey Bay; and in the Atherton Tableland area, where the focus was almost entirely on *E. tereticornis* (locations: Atherton, Bingham Road, Durrambdi bridge, Ervinebank, Gympie, Herberton, Hervey Bay, Mareeba, Walkamin, Yungaburra). During the second and the third expeditions we revisited *E. camaldulensis* trees growing along the Murrumbidgee River and canals linked to this river near Wagga Wagga (NSW).

Occurrence of Leptocybe invasa galling material in Australia

There is a rich fauna of gall inducing arthropods on *Eucalyptus* in Australia. The largest group of gall inducers are wasps in the family Eulophidae, mainly in the genus *Ophelimus* and several genera of Tetrastichinae (La Salle 2005). One cannot predict the gall inducer based on gall morphology. As an example, *Ophelimus* species induce galls ranging from small blister type galls on leaves containing a single individual (e.g. *O. maskelli*, Protasov *et al.* 2007b) to large woody swelling on twigs containing many individuals.

Galling material appearing similar to that induced by *L. invasa* was rarely observed in *E. rudis* forests in Western Australia, or in areas surveyed in northern Victoria and western NSW. For example, only a few such galls induced on leaves or shoots of *E. camaldulensis* were collected along the banks of the Murrumbidgee River near Wagga Wagga, whereas galls of *Ophelimus maskelli* (whose parasitoids were also under study) could be found easily. However, in the absence of reared material, there is no proof that the few galls that closely resembled those of *L. invasa* were, in fact, induced by this wasp species. Such galling material was hardly found on young seedlings of *E. rudis* that developed after a forest fire in the surveyed locations in Western Australia, or in young experimental plots of hybrids of *E. camaldulensis* in NSW.

Other kinds of galling material could easily be found on young trees, and only seldom on adult trees, in those areas; these were mainly induced by other eulophid wasps and gall midges, which were not identified. Also detected on young plants were many of the small blister-type galls similar to those produced by *O. maskelli*.

Galls resembling those produced by *L. invasa* were frequently found in Queensland, between Gympie and Hervey Bay, and on the Atherton Tableland. In both studied areas, frequent occurrences of suitable galling material were found on young *E. tereticornis* trees either in 3- to 4-yr-old plantations, or on young trees of a similar age growing along small streams or in dry small river beds. In these cases the galls had developed mainly on the stems of the small branches and only rarely on the leaves, which were, in many cases, either damaged by sawfly larvae or covered with small, blister-type galls. In older plantations the occurrence of these galls was much less frequent, and very few galls were actually sampled. In plantations of adult trees such galling material was hard to find, even in several hours of searching by three persons.

Parasitoid collection sites

The original stocks of *Selitrichodes kryceri* and *Quadrastichus mendeli* were reared from *L. invasa* galls on *Eucalyptus tereticornis* collected from young trees growing in dry steam beds or on regenerating sites in several locations in Queensland. Galls were usually collected 30–60 cm above ground. Suitable galling material was found: near Bingham Road, 30 km west of Hervey Bay on two sites (25°20'S, 152°52'E elevation 19 m, and 26°05'S, 152°34'E elevation 76 m); on the Atherton Tableland along the road from Herberton to Irvinebank (between 17°22'S, 145°22'E, elevation 933 m, and 17°25'S, 145°11'E, elevation 840 m); and Mareeba, Mareeba Sewerage effluent trail, near Adil Rd 16°57'S, 145°23'E elevation 396 m. Because of the relatively small number of specimens of galling materials that were removed from the collection sites, we combined the emerging parasitoids from the four main collection areas (on other sites similar galling material, if found, was rather rare).

Among the several chalcidoids that emerged from the collected material, and were placed on *E. camaldulensis* that had been galled by *L. invasa*, only *S. kryceri* and *Q. mendeli* were recovered in sufficient numbers to establish rearing colonies. At that time, most of the eulophid parasitoids that emerged from the galls were

Taxonomy of Leptocybe invasa parasitoids

The two species described in this paper, *Quadrastichus mendeli* and *Selitrichodes kryceri*, are both in the Eulophidae subfamily Tetrastichinae. Australian Eulophidae were treated by Bouček (1988), who provided a key to all genera. Unfortunately, concurrent to Bouček's studies, Graham was revising European Tetrastichinae, and provided a much revised classification of European genera (Graham 1987), which appeared after Bouček's work had already gone to press. For this reason, some genera treated by Bouček (1988) do not reflect current generic interpretations in the Tetrastichinae (Graham 1987, 1991; La Salle 1994; Schauff *et al.* 1997). In particular, Bouček treated several genera as synonyms of *Aprostocetus* which need re-examination in light of these subsequent studies.

Terminology used in this paper is taken from Gibson (1997) and Graham (1987). OOL, ocellar–ocular distance; POL, post-ocellar distance; CC, costal cell; SMV, submarginal vein; MV, marginal vein; STV, stigmal vein; PMV, postmarginal vein; PDL, pedicel; F1–3, funicular segment 1–3; A1–3, anellus 1–3; C1–3, claval segment 1–3.

Acronyms used in the text are as follows. ANIC, Australian National Insect Collection, CSIRO Entomology, Canberra, Australia; BMNH, Natural History Museum, London, UK; QMB, Queensland Museum, Brisbane, Australia; USNM, United States National Museum of Natural History, Washington, D.C., USA.

Girault types and dates of publication. A.A. Girault published extensively on Australian Chalcidoidea, several thousand species. As part of this study, types of species of Tetrastichinae described by Girault and stated as being associated with galls were borrowed and studied, and several of his genera and species are discussed in this paper. Unfortunately, the identity of his type specimens is not always straightforward (Dahms 1978). A series of works has discussed the identity of his Australian types and resolved most of the confusion regarding them (Dahms 1983, 1984, 1986).

An additional challenge when studying Girault species is that in many cases the type material is in extremely poor condition (Dahms 1978). Specimens are often fragmented and/or damaged, with parts missing or mounted on poor quality slides. This has prevented us from being able to fully understand and discuss all of the species in this paper, and makes some of the decisions tentative.

Due to the Principal of Priority (ICZN 1999), it is essential to know the exact dates of Girault's publications (for example, Girault published 49 papers in 1913). Publication dates for all of his papers are listed by Dahms (1978), who also ordered all of Girault's papers by date of publication. The numbers in brackets given in this paper refer to the numbering given in Dahms (1978).

Taxonomic decisions. All taxonomic decisions in this paper should be attributed to Kim & La Salle.

Differences between Quadrastichus mendeli and Selitrichodes kryceri

Although *Q. mendeli* and *S. kryceri* are placed in different genera, they are superficially very similar in appearance, being mainly yellow with black markings (see Figs 1–3), and they could easily be confused. The following characters are presented to facilitate their identification by non-specialists. Note that these characters are only to be used to distinguish the two parasitoids imported and released in the Mediterranean Basin.

Quadrastichus mendeli	Selitrichodes kryceri
Submarginal vein with 1 dorsal seta (Fig. 4)	Submarginal vein with 2 dorsal setae (Fig. 15)
Antenna with all funicular segments longer than wide (Fig. 5)	Antenna with funicular segments quadrate to wider than long (Fig. 10)
Uniparental	Biparental

Unfortunately, the morphological characters can still be difficult to see without microscopic examination. Other characters might be useful, but are not totally reliable. For example, *S. kryceri* generally has the gaster a dusky yellow, with 5–6 dark bands (Fig. 2), while *Q. mendeli* has the gaster brighter yellow, usually with 3–4 dark bands (Fig. 1). However, this character is variable, and in some specimens of *S. kryceri* the bands can be completely lacking (Fig. 3). Similarly, in *Q. mendeli* the gaster generally appears longer and narrower than in *S. kryceri* (compare Figs 1 and 2); however there is overlap in this character and measurements cannot be provided which will reliably separate all specimens of these species.



FIGURES 1–3. Habitus. 1. *Quadrastichus mendeli* $^{\circ}$; 2. *Selitrichodes kryceri* "dark" specimen $^{\circ}$; 3. *Selitrichodes kryceri* "light" specimen $^{\circ}$

Genus Quadrastichus

Quadrastichus was described by Girault (1913[167]), and synonymised with Aprostocetus by Bouček (1988). It was subsequently removed from synonymy by Graham & La Salle (1991), and given revised status as a senior synonym of Cecidotetrastichus Kostjukov. Generic keys which would allow identification to Quadrastichus are provided by Graham (1987 as Cecidotetrastichus; 1991), La Salle (1994), and Schauff et al. (1997). A complete synonymy list for Quadrastichus is given by Graham (1991).

Many species of *Quadrastichus* are associated with galls, usually as endoparasitoids of Diptera Cecidomyiidae and Hymenoptera Cynipidae, and one European species *Q. sajoi* (Szelényi) has larvae which are predatory on eriophyid mites within galls (Graham 1991; La Salle 1994; Noyes 2003). One species has recently been recorded as an invasive pest which induces galls on coral trees (*Erythrina* spp.: Fabaceae) (Kim *et al.* 2004).

In addition to being associated with galls, species of *Quadrastichus* have varied biologies, and other hosts include Coleoptera Curculionidae and Buprestidae (Graham 1991; La Salle 1994; Noyes 2003), and several Asian species are parasitoids of leafmining Agromyzidae (Reina & La Salle 2003, 2004).

Although at this time, there are only two Australian species recognized in the genus *Quadrastichus* (*nigrinotatus* Girault, *mendeli* sp.n.), results from surveys indicate that there may be many more species in this genus associated with galls on *Eucalyptus*.

Quadrastichus mendeli Kim and La Salle sp. nov. (Figs 1, 4–9)

Female Length 1.15–1.35 mm. Antenna light brown (or testaceous). Body mainly yellow with dark brown markings; on ocellar triangle, median area of pronotum, latero-posterior corner of pronotum just in front of prothoracic spiracle, apex of axilla, lateral panel of metanotum, median area of propodeum, transverse stripes on gastral tergites 2–4. Legs pale.

Head (Figs 6,7). POL about 2.8 times as long as OOL on shriveled head. Frons with a median area dorsally, bordered laterally by sutures which extend from frontal suture halfway to level of toruli. Vertexal suture very weak and extending from lateral ocellus to eye. Frons with median area but without median carina. The ventral margin of torulus slightly lower than level of ventral margin of eyes. Subantennal groove (hard to see under a microscope due to bright body color) present as a fine line beneath torulus, curved outwardly and extending over half of the distance from torulus to clypeal margin. Gena swollen and malar sulcus distinctly curved. Anterior clypeal margin subtruncate, only with a small lobe slightly protruding.

Antenna (Fig. 5) with three funicular segments and one large anellus. All funicular segments longer than wide and almost equal in length and width; relative length of funicular segments to pedicel as follows: PDL: F1: F2: F3 = 1: 0.7–0.9: 0.7–0.9: 0.7–0.8. Claval segment between C2 and C3 oblique; C3 very short (terminal spine difficult to see due to sensillae on C3). Scape reaching to vertex, but not extending over vertex.

Mesosoma (Fig. 8). Pronotum about 0.3 the length of the mid lobe of mesoscutum in dorsal view. Mid lobe of mesoscutum with distinct median line and with 3–4 adnotaular setae on each side. Scutellum wider than long (L/W = 0.7); submedian lines and sublateral lines present. 2 pairs of setae on scutellum, anterior seta situated slightly behind midlength of scutellum. Mesosternum nearly flat in front of trochantinal lobe; precoxal suture weak and extending about 0.3–0.4 length of mesopleuron. Dorsellum semicircular in shape and about 0.3 the length of scutellum. Propodeum about 0.5 the length of dorsellum and nearly smooth without distinct median carina or paraspiracular carina. Propodeal spiracle partially covered by a raised lobe of callus. Propodeal callus with 2 setae.

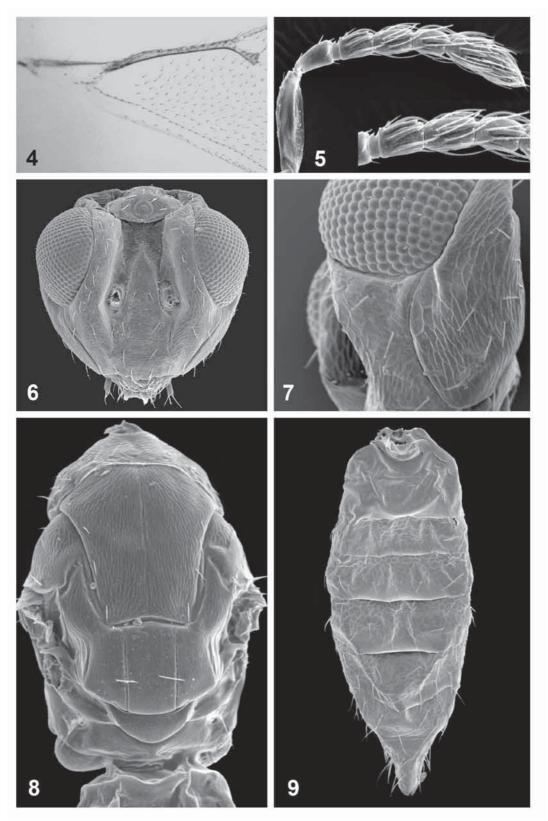
Fore wing (Fig. 4). Submarginal vein with 1 seta, situated slightly basal to the middle. Costal cell without setae. Parastigma and stigmal vein without a hyaline break. Postmarginal vein rudimentary. Relative length of wing veins as follows: CC: MV: STV: PMV = 3.1–3.4: 3.3–3.5: 1: 0.1–0.2. Cubital line of setae extending all the way to basal vein, closing speculum. Bare area of speculum extending to about half the length of the MV. Two small bare circular areas present apical to the stigmal vein, from PMV to uncus and from uncus to the apical end of STV.

Gaster (Fig. 9). Slightly longer than the head plus mesosoma. Hypopygium extending about 0.3–0.4 the length of gaster, reaching up to the posterior margin of the third gastral tergite. Cercus with 3 setae, the longest one slightly curved and about 1.3 as long as the others, which are subequal in length. Ovipositor sheath slightly protruding, very short in dorsal view.

Male. Unknown.

Etymology. The species is named for Dr Zvi Mendel, for his dedication to finding sustainable control measures for *Leptocybe invasa*.

Material examined. Holotype ♀: Australia, Queensland, Mareeba, 14.x.2005, J. McDonald & H. Nahrung, ex galls on *E. camaldulensis* x *grandis* (ANIC).



FIGURES 4–9. *Quadrastichus mendeli* ⁹. 4. Base of fore wing; 5. Antenna; 6. Head, frontal view; 7. Malar sulcus; 8. Mesosoma; 9. Gaster.

Paratypes: Same data as Holotype (1 $\,^{\circ}$ ANIC); Quarantine Reared, Bet Dagan, Israel, 20.viii.2007 (originally Australia, from locations given above under parasitoid collection sites) (65 $\,^{\circ}$ as follows. 40 $\,^{\circ}$ ANIC; 5 $\,^{\circ}$ each: QMB, BMNH, USNM, CNC, PPRI).

Discussion. This new species fits the definition of the genus provided by Graham (1991): SMV with 1 dorsal seta, antenna with all funicular segments longer than wide and with 1–3 anelli in female and gaster longer than the head plus mesosoma. Although this species doesn't match well with the keys for European species which was provided by Graham (1991), the species would run to the *anysis*-group of *Q. anysis* (Walker) as follows: frons with median area but without median carina, gena (slightly) swollen, malar sulcus (only slightly) curved, malar sulcus without a large subtriangular fovea just beneath eye, clypeal margin truncate. However, the species differs from all other *Quadrastichus* on the basis of characters as follows: malar sulcus rather strongly curved, C3 very short and claval sutures oblique, subantennal groove distinct and curved outwardly, clypeal margin subtruncate with a small lobe protruding in the middle, and mid lobe of mesoscutum with 3–4 adnotaular setae. Additionally, this new species appears to have a transverse frontal suture extending between the eyes just ventral to the median ocellus, with a longitudinal frontal suture reaching from the transverse suture to the torulus.

Genus Selitrichodes

Selitrichodes Girault, stat. rev.

Selitrichodes Girault, 1913[145]: 104–105. Type species: Selitrichodes fasciativentris Girault, original designation. Stat.rev.

Epomphaloides Girault, 1913[156]: 49–50. Type species Epomphaloides flavus Girault, original designation. **Syn. n.** Zagrammosomoides Girault, 1913[146]: 177. Type species Zagrammosomoides fasciatus Girault, original designation, **Syn.n.**

Diagnosis. SMV usually with 2 or 1 dorsal setae. PMV distinct, usually about 0.4–0.5 the length of STV. Propodeum without a raised lobe of the callus which partially overhangs the outer rim of the spiracle. Cercal setae short and subequal in length. Mesosternum anterior to the trochantinal lobe convex and without a precoxal suture. Malar sulcus generally curved, and the gena may be somewhat swollen. All funicular segments subquadrate or slightly transverse. Postmarginal vein distinctly developed, although shorter than the stigmal vein. Non-metallic (mainly yellow with black markings). Males (of at least some species) with 3 funicular segments.

Discussion. Graham (1987) defined the genus *Aprostocetus* mainly on possessing the following characters: propodeum with a raised lobe of the callus which partially overhangs the outer rim of the spiracle, one of the cercal setae distinctly longer than the others and sinuate, submarginal vein with 3 or more setae, mesosternum in front of the trochantinal lobe generally flat and with a preocoxal suture, and malar sulcus generally straight or only slightly curved. This generic concept has been used by subsequent authors (Graham 1991; La Salle 1994; Schauff *et al.* 1997).

Bouček (1988) mentioned the presence of a group of species which he placed in *Aprostocetus* which had cercal setae short and the postmarginal vein distinctly developed, although shorter than the stigmal vein. He suggested that some of these groups may need to be treated as separate genera. Several of the forms which are found associated with galls on *Eucalyptus* fall into this category, including the type species of *Selitrichodes*, *Zagrammosomoides* and *Epomphaloides*.

Diagnostic characters for *Selitrichodes* have been given above. Differences between *Selitrichodes* and *Aprostocetus* are that *Selitrichodes*: lacks a raised lobe of the callus which partially overhangs the outer rim of the spiracle, has all the cercal setae short and subequal in length, has 2 setae on the submarginal vein, has the mesosternum in front of the trochantinal lobe convex and without a precoxal suture, and the malar sulcus generally curved. These differences are enough to recognize *Selitrichodes* as a valid genus, which is distinct from *Aprostocetus*. Additional characters for *Selitrichodes* are that all funicular segments are subquadrate or

slightly transverse, and the postmarginal vein distinctly developed, although shorter than the stigmal vein. Males for *Selitrichodes kryceri* have only 3 funicular segments (most tetrastichine males have 4 funicular segments). Males are unknown for most *Selitrichodes*, and it is not clear how widespread this character is.

Many of the characters which define *Selitrichodes* are similar to those seen in the mainly Holarctic genus *Baryscapus* Förster. *Baryscapus* is largely absent in the Australian fauna (Bouček 1988; Noyes 2003), with the only recorded species, *B. galactopus* (Ratzeburg), almost certainly introduced. The main character by which *Baryscapus* can be separated from *Selitrichodes* is that *Baryscapus* are always metallic in coloration, and *Selitrichodes* are non-metallic (mainly yellow with black markings).

We could find no significant differences between *Selitrichodes* and *Epomphaloides*, and *Epomphaloides* is treated as a synonym with *Selitrichodes*. The only significant difference between *Zagrammosomoides* and *Selitrichodes* is that *Zagrammosomoides* has an elongate mesoscutum, which is fully twice as long as the scutellum. Both *Selitrichodes* and *Zagrammosomoides* have an official publication date of 30 June 1913 (Dahms 1978). Acting under the principle of first reviser, we consider *Selitrichodes* to have priority. An additional group of species generally agree with *Selitrichodes*, but differ in having only a single seta on the submarginal vein. Since this is the only difference, these species (*auriflavus, consobrinus, secus, varigatus*) are also placed in *Selitrichodes*.

Included species

auriflavus (Girault), comb.n.

Tetrastichodes auriflavus Girault 1915[230]: 220. Syntypes, 2[♀], 1♂, Gordonvale (Nelson), near Cairns, Queensland, (QM, Hy 2552) [examined].

Aprostocetus auriflavus (Girault): Bouček, 1988: 678.

consobrinus (Girault), comb.n.

Tetrastichodes consobrinus Girault 1913[167]: 209, 211. Syntypes, 3♀, Gordonvale (Nelson), near Cairns, Queensland (QM, Hy 1772) [examined]

Aprostocetus consobrinus (Girault): 679.

fasciativentris Girault

Selitrichodes fasciativentris Girault, 1913[145]: 105. Syntypes, 4º, NSW, exact locality unknown (QM, Hy 1198) [examined]

Selitrichodes fasciativentris Girault: Girault, 1913[167]: 226; Girault, 1915[230]: 233.

Aprostocetus fasciativentris (Girault): Bouček, 1988: 680.

fasciatus (Girault) [Zagrammosomoides]—see multifasciatus

flavus (Girault) [Epomphaloides]

Epomphaloides flavus Girault, 1913[156]: 49–50. Holotype ♀, Gordonvale (Nelson), near Cairns, Queensland, (QM Hy1842) [examined].

Epomphaloides flavus Girault: Girault, 1913[167]: 106-107; Girault, 1915[230]: 251.

Aprostocetus flavus (Girault): Bouček, 1988: 680.

flavus (Girault) [Selitrichodes]—see giraulti

giraulti Kim & La Salle, nom. nov.

Replacement name for *Selitrichodes flavus* Girault (10 December 1913), not *Epomphaloides flavus* Girault (30 September 1913).

Selitrichodes flava(!) Girault, 1913[167]: 226–227. Holotype 9, Gordonvale (Nelson), near Cairns, Queensland, (QM

Aprostocetus flavus (Girault): Bouček, 1988: 680.

kochi (Girault) [Tetrastichodes]—see variegatus

kryceri Kim & La Salle sp. nov.

multifasciatus (Girault), comb.n.

Zagrammosomoides fasciatus Girault, 1913[146]: 178. Syntypes, 10♀, 62♂, Gordonvale (Nelson), near Cairns, Queensland, (QM Hy1169) [examined]. Note discussion by Dahms (1984: 589–590) concerning the tangled nomenclatural history of this species.

Tetrastichodes (*Zagrammosomoides*) *multifasciatus* Girault, 1915[230]: 219. Replacement name for *Z. fasciatus* Girault nec *T. fasciatus* Ashmead, 1894.

Aprostocetus multifasciatus (Girault): Bouček, 1988: 683.

quinqnigrimaculae (Girault), comb.n.

Tetrastichodes quinquigrimaculae Girault, 1915[230]: 221. Holotype ♀, Victoria, Melbourne (QM, Hy 2553) [examined]

Aprostocetus quinquigrimaculae (Girault): Bouček, 1988: 684.

secus (Girault), comb.n.

Tetrastichodes secus Girault 1915[230]: 220. Syntypes, 4^o, Gordonvale (Cairns), Queensland, (QM, Hy 3462) [examined].

Aprostocetus secus (Girault): Bouček, 1988: 685.

tricolor (Girault), comb.n.

Tetrastichella tricolor Girault 1915[230]: 250. Holotype ♀, Gordonvale (Cairns), Queensland, (QM, Hy 2625) [examined].

Aprostocetus tricolor (Girault): Bouček, 1988: 685.

variegatus (Girault), comb.n., stat.rev.

Epomphaloides variegatum Girault 1915[230]: 252. Holotype ♀, Gordonvale, near Cairns, Queensland, (QM Hy2630) [examined].

Tetrastichodes kochi Girault 1935[445]: 4. Unnecessary substitute name. Girault (1935) transferred E. variegatus to Tetrastichodes, and supplied the replacement name T. kochi as variegatus was preoccupied. Although not specifically stated, he could only have thought that the homonymy was caused due to his considering that S. varigatus properly belonged in Tetrastichodes (see Dahms, 1986: 624, 625-6 under Epomphaloides variegatum and Selitrichodes varigatus). As varigatus and variegatus must be considered as distinct names which do not compete for homonomy, kochi becomes an unnecessary substitute name.

Aprostocetus kochi (Girault): Bouček, 1988: 682.

varigatus Girault, stat.rev.

Selitrichodes varigatus Girault 1913[167]: 226. Holotype ♀, Gordonvale (Nelson), near Cairns, Queensland, (QM Hy1909) [examined].

Aprostocetus variegatus (Girault): Bouček, 1988: 686. Incorrect subsequent spelling of varigatus. See discussion at variegatus

Although exact biology and host plants are unknown for most species, many of them were associated with galls. Almost all of the included species were collected from more or less the same area in Queensland, and indications from rearing activities are that this may be a large group in Australia.

(Figs 2, 3, 10–17)

Female Length 1.35–1.75 mm. Color patterns are variable: body almost completely yellow or mainly yellow with dark brown markings. If with black markings, then as follows: scape dorsally black, median and lateral ocelli, on anterior half and each latero-posterior corner of pronotum just in front of prothoracic spiracle, apical half of axilla, anterior area between submarginal lines of scutellum, lateral panel of metanotum, medial area of propodeum, from Gt2 to Gt5 of gaster with a dark brown stripe dorsally. At a minimum, the pale forms will always have the following black or dark brown: a small spot on the lateral corner of the pronotum, a small spot around each ocellus, a thin transverse stripe on the hind margin of the propodeum. All legs testaceous.

Head (Figs 12–14). Ocellar triangle without grooves; sometimes grooves can be seen only on a shrunken specimen. POL about 5 times as long as OOL. Frontal suture transverse medially with lateral sides turning ventrally, placed ventral to median ocellus, separated from the median ocellus by about its diameter, . Frons with median carina extending halfway to toruli and a small transverse crack-like suture present at the end of the carina. The ventral margin of torulus lower than ventral margin of eye. A broad depression below torulus extending close to clypeus and with some pilosity on the depression. Gena swollen and with distinctly curved malar sulcus. Clypeal margin bidentate.

Antenna (Fig. 10) with 3 funicular segments and 3 anelli; dorsal side of anellus shorter than ventral side; A2 very thin and generally not visible in dorsal view. Funicular segments with dorsal side slightly shorter than ventral side, from subquadrate to slightly transverse: length/width ratio of F1 0.8–0.89; F2 0.75–0.85; F3 0.62–0.68 (ventral side measured for length). Relative length of funicular segments to pedicel as follows: PDL: F1: F2: F3 = 1: 0.17–0.21: 0.19–0.2: 0.18–0.19. Clava without distinct terminal spine (or very hard to see because of sensilla around the apical end of C3) and claval segments slightly asymmetrical with its sutures rather oblique; C3 very short and its end broad, not tapering apically and with micropilose area (MPA) dorsoapically. Scape flat and expanded from base to apical end; not exceeding above the vertex.

Mesosoma (Fig. 16). Pronotum very short medially in dorsal view. Mid lobe of mesoscutum with very weak median line and with one row of 7–9 adnotaular setae on each side. Mesosternum convex just in front of the trochantinal lobes and without precoxal suture. Scutellum with all setae located behind middle. Dorsellum semicircular. Propodeum medially shorter than dorsellum in dorsal view; anterior and posterior margin almost abutting, so that median carina absent. Propodeal spiracle with its whole rim exposed and separated from the anterior margin of propodeum by its longest diameter; spiracle longer than propodeum, about 2 times as long as propodeum in dorsal view. Paraspiracular carina absent. Callus with 2 setae. Hind corner of propodeum with very small protuberance projected posteriorly.

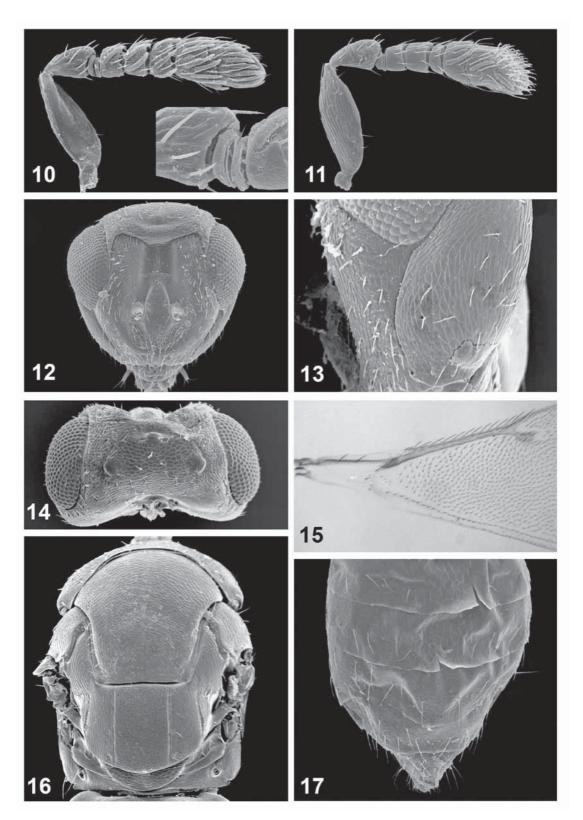
Fore wing (Fig. 15). Submarginal vein usually with 2 dorsal setae, rarely 1 or 3 on one wing. Costal cell mostly asetose except usually with one or two very small dorsal setae just in front of marginal vein. Parastigma with a hyaline break, no hyaline break on stigmal vein. Relative length of wing veins to stigmal vein as follows: CC: MV: STV: PMV = 4.5–4.6: 4.8–5.0: 1: 0.5–0.6. Speculum small and open posteriorly, not closed by basal and cubital setal lines; cubital line close to but not reaching to the level of basal line; speculum with a few small setae on underside of wing. Small patch without pilosity present apical to STV and PMV. Wing disk beyond speculum densely pilose.

Gaster (Fig. 17) slightly longer than head plus mesosoma. Hypopygium reaching to level of 4th gastral tergite. Cercus with 3 setae subequal in length and slightly curved. Ovipositor sheath slightly protruding, very short in dorsal view.

Male Length 1.0–1.15 mm. Body color patterns similar with female, but with more black markings on vertex, mid lobe of mesoscutum, scutellum, propodeum and gaster.

Antenna (Fig. 11) with 3 anelli and only 3 funicular segments; F1 virtually quadrate and as long as broad; F2 subquadrate and very slightly wider than long; F3 distinctly shorter than the other segments and wider than

long. Each successive segment slightly getting broader. Funicle and clava without compact subbasal whorls of long setae MPA on clava bigger than that of female. Ventral plaque about 0.3–0.4 length of scape and the lower margin of the plaque located nearly in the middle of the scape.



FIGURES 10–17. *Selitrichodes kryceri*. 10. Antenna $\,^{\circ}$; 11. Antenna $\,^{\circ}$; 12. Head $\,^{\circ}$, frontal view; 13. Malar sulcus $\,^{\circ}$; 14. Head $\,^{\circ}$, dorsal view; 15. Base of fore wing, $\,^{\circ}$; 16. Mesosoma $\,^{\circ}$; 17. Gaster $\,^{\circ}$.

Etymology. The species is named for Joe Krycer, Jewish National Fund (KKL) of Australia, who believed in this project from the beginning.

Material examined. Holotype ♀: Australia, Queensland, Mareeba, 14.x.2005, J. McDonald & H. Nahrung, ex galls on *E. camaldulensis* x *grandis* (ANIC).

Paratypes (32° , 19°): Same data as Holotype (17° , 9° ANIC; 3° , 2° each: QMB, BMNH, USNM, CNC, PPRI). Quarantine Reared, Bet Dagan, Israel, (originally Australia, from locations given above under parasitoid collection sites) (11° , 11° ANIC).

Discussion

Due to the poor condition of the Girault type material, it is difficult to compare *S. kryceri* to other species of *Selitrichodes*. Because it has two setae on the SMV, it can be separated from those species which only have a single seta (*auriflavus*, *consobrinus*, *secus*, *varigatus*). It can be separated from *S. multifasciatus* by not having the mesoscutum elongate and nearly twice the length of the scutellum.

The following characters in combination should serve to distinguish it from other described species of *Selitrichodes*: Transverse dark stripes (when present) on gaster in the form of individual lines on gastral tergites rather than a single broad line covering several gastral tergites; mesosomal colour ranging from predominantly yellow to yellow with distinct dark brown markings, never uniformly brown; always with a dark spot around the ocelli and a dark spot at the lateral corner of the pronotum; POL about 5 times as long as OOL; speculum small and open posteriorly, not closed by basal and cubital lines of setae; cubital line approaching but not reaching basal line; speculum with a few small setae on underside of wing.

Biological studies on *Leptocybe invasa* parasitoids

Rearing procedure and facilities

Parasitoids were released onto saplings of E. camaldulensis on which about 25% of the branches and their leaves were galled by L. invasa, in $30 \times 30 \times 90$ -cm Plexiglas cages. The age of the galls ranged from 50 to 90 days (mature larvae and prepupae). In the quarantine facility the cages were kept in a closed room. Later, in the mass-rearing stage, they were kept under semi-controlled temperature in greenhouses, at the Volcani Center, Bet Dagan, in the central Coastal Plain in Israel.

Two sources of infested saplings were used. The first was a supply of selective infested saplings with *L. invasa* galls from the KKL Forest Department nursery in Gilat. A further supply of galled plants was produced by artificial infestation of saplings exposed to *L. invasa* in greenhouse conditions; the wasps for this purpose were obtained from infested material collected in heavily infested plantations, mainly in the Bet Shean Valley.

Selitrichodes kryceri is a biparental species whereas Quadrastichus mendeli is uniparental. Both are small, about 1 mm in body length.

Effect of host development stage on offspring production and development time

Parasitoid development was studied by dissecting several dozen randomly chosen galls of *L. invasa*, 45–65 days after gall inducer oviposition, on leaves that had been removed from *E. camaldulensis* saplings about 20 days after the plant had been exposed to the parasitoid species.

Five groups of five to ten 18-month-old saplings were exposed to L. invasa at 24 h post-emergence for 24 h, in ventilated Plexiglas cages. Ten L. invasa per sapling were introduced into each cage on a range of dates in order to produce a range of gall ages: (0) uninfested saplings, (A) 15 days (egg to hatching), (B) 50 days (young larvae), (C) 75 days (mature larvae), (D) ~100 days (prepupae to pupae), and (E) 115 days (callow

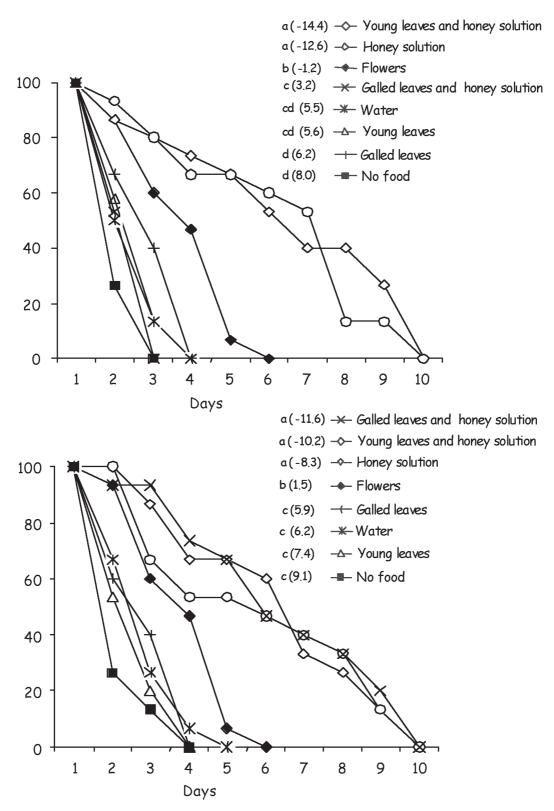


FIGURE 18. Survival patterns of females (the upper graph) and males *Selitrichodes kryceri* at 25° C, as related to feed alternatives. Each treatment of each wasp sex involved 20 wasps. In parentheses are the values of Log-Rank statistics: values with the same letter are not statistically different (P = 0.05) according to a close test procedure.

adult before emergence). Adult emergence was recorded 122.5 ± 3.6 days after the infestation, and ranged from 110 to 130 days. To each of the cages we introduced two pairs of *S. kryceri* or two females of *Q. mendeli*, for 24 h. The test was conducted in a ventilated greenhouse at an average temperature of 28.1° C and relative

humidity ranging from 40 to 70%. To obtain emerging adults, about 20–22 days after exposure of the galled saplings to parasitization, the relevant branches were removed and put in sealed polyethylene emergence boxes. The emerging parasitoids were collected daily. The number of *L. invasa* gall units exposed to parasitisation (determined using the regression equation between the wasp pupae chambers and the length of the gall, Mendel *et al.* 2004), the number of emerging adults, and the development time of the tested parasitoids in each of the treatments were determined. The mortality percentage for *L. invasa* was calculated from the number of emerging parasitoids divided by the total number of emerging wasps (gall formers + parasitoids) for each cage.

Both *S. kryceri* and *Q. mendeli* are solitary parasitoids. It was not determined whether the host was killed immediately or shortly after parasitization. The entire development was completed in 30 days (Tables 1, 2). Dissecting several dozen randomly chosen galls of *L. invasa* suggests that both parasitoid species are ectoparasitoids.

The two species required the same host developmental stages (Tables 1, 2). Successful development occurred on both young and mature host larvae (50 and 75 days, respectively, post oviposition by *L. invasa*), and we suspect that the few parasitoids that emerged from galls that harbored prepupae (~100 days after parasitization) had actually developed on somewhat younger hosts.

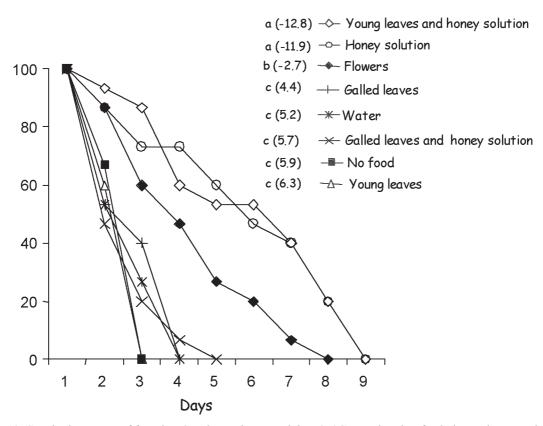


FIGURE 19. Survival patterns of females *Quadrastichus mendeli* at 25°C, as related to feed alternatives. Each treatment involved 20 wasps. In parentheses are the values of Log-Rank statistics: values with the same letter are not statistically different (P = 0.05) according to a close test procedure.

Adult longevity

The longevity of the studied parasitoids was determined under eight feeding treatments: (i) no food; (ii) water; (iii) young healthy foliage of *E. camaldulensis*; (iv) honey solution, i.e., 1:1 solution in distilled water; (v) combination of treatments iii and iv; (vi) fresh *E. camaldulensis* flowers; (vii) galled foliage and twigs of *E. camaldulensis*, (stage C, 75 days post *L. invasa* oviposition); and (viii) combination of treatments iv and vii.

TABLE 1. Parasitism percentages and development duration of *Selitrichodes kryceri* on *E. camaldulensis* saplings bearing various gall stages of *L. invasa*. Values are presented as mean \pm 1SD.

Development stage (days after oviposition)	_	Number of emerging <i>L. invasa</i>	Number of emerging <i>S. kryceri</i>	Development time (days) of <i>S. kryceri</i>	e % parasitism
0	0	0	0	0	0
A (15)	12.0 ±2.7*	9.6 ± 2.9	0	0	0
B (50)	11.8 ± 5.5	3.0 ± 3.5	7.0 ± 3.2	30.8 ± 0.5	59.0 ± 8.4
C (75)	7.6 ± 4.9	3.2 ± 3.9	3.2 ± 1.6	31.0 ± 0.7	46.2 ± 17.3
D (100)	15.0 ± 7.5	12.2 ± 4.7	0.8 ± 1.8	32**	3.2 ± 7.1
E ((115)	11.8 ± 3.1	10.4 ± 2.7	0	0	0

^{*} Number of scars at the oviposition points

TABLE 2. Parasitism percentages and development duration of *Quadrastichus mendeli* on *E. camaldulensis* saplings bearing various gall stages of *L. invasa*. Values are presented as mean \pm 1SD.

Development stage (days after oviposi-	ě.	Number of emerging <i>L. invasa</i>	Number of emerging <i>Q. mendeli</i>	Development time (days) of <i>Q. mendeli</i>	% parasitism
tion)	units per plant	ing L. mvasa	mg g. menuen	(days) of Q. menaen	
0	0	0	0	0	0
A (15)	11.6 ±4.3*	16.0 ± 5.1	0	0	0
B (50)	7.0 ± 1.8	0.6 ± 09	5.8 ± 1.5	30.0 ± 1.4	84.2 ± 11.4
C (75)	8.4 ± 1.1	2.2 ± 1.1	5.2 ± 1.3	29.0 ± 2.3	61.8 ± 11.9
D (100)	6.8 ± 1.2	5.8 ± 1.8	0.6 ± 0.9	28**	7.9 ± 12.5
E ((115)	8.0 ± 0.7	$7.4\pm\!0.5$	0	0	0

^{*} Number of scars at the oviposition points

Thirty wasps of each sex of *S. kryceri* and females of *Q. mendeli* were placed in 95-mm-diameter Petri dishes (five wasps per dish) fitted with a filter-paper disk. The water or the honey solutions were sprayed along a narrow strip on the cover of each Petri dish, and the food supplies, including water and leaf materials, were renewed daily. The wasps for testing were collected on the day of emergence, removed with a fine brush and placed in a Petri dish, males and females separately. Wasp mortality was recorded daily. The test was conducted at 25°C and 70–75% relative humidity. Survival data were analyzed with the Life Test Procedure software package of the SAS Institute (SAS Institute, 2002). Empirical survival distributions were fitted to the various treatments. The homogeneity of the survival distributions was tested with log-rank statistics; mean survival ± SE values for all treatments were also calculated.

The survival patterns of adult wasps of both species differed significantly among the feeding treatments (Figs. 18, 19), ranging from 3 to 6 days. *S. kryceri* adults could be divided into three groups of survivors. The greatest longevity of the females was among those that received honey and water solution or young healthy foliage + honey solution – estimated 50% survival (i.e., 50% ES, mean number of days \pm SE) was 6.5 ± 0.7 days. Females supplied with flowers survived significantly less – 50% ES was 4.0 ± 0.7 days – but significantly more than those receiving other feeds (i.e., water, young healthy foliage, galled foliage alone, or galled leaves + honey) with mean 50% ES = 2.6 ± 0.2 days. The greatest longevity of the males was among those that were offered honey and water solution, young healthy foliage + honey solution, or galled leaves + honey, with mean 50% ES of 6.4 ± 0.7 days. Males that were supplied with flowers survived significantly less, 50%

^{**} The parasitoid emerged from only one of the saplings

^{**} The parasitoid emerged from only one of the saplings

ES = 4.1 ± 0.3 days, but significantly more than those receiving other feeds (i.e., water, young healthy foliage, or galled foliage alone) (Fig. 18) which had a mean 50% ES = 2.8 ± 0.2 days.

Q. mendeli females could be clearly divided into three groups of survivors. The greatest longevity was among those that received honey and water solution or young healthy foliage + honey solution – their 50% ES was 6.0 ± 0.6 days. Females supplied with flowers survived significantly less than these – 50% ES = 4.5 ± 0.5 days – but significantly more than those receiving other feeds (i.e., water, young healthy foliage, galled foliage alone or galled leaves + honey) which had a mean 50% ES = 2.7 ± 0.2 days. (Fig. 19).

Efficacy of Leptocybe invasa parasitoids

Release and recovery of S. kryceri and Q. mendeli in E. camaldulensis stands

Adult wasps of the two species that had been collected from the emergence boxes during 2–3 days were allowed to feed on honey and water solution, and were released on the next day in three sites planted with *E. camaldulensis*: Bet Dagan, Segula (Coastal Plain) and Nir David (Bet Shean Valley). Information about the release number and the sample size for the recovery is presented in Table 3.

TABLE 3. Information on the release and the recovery of two parasitoids of *L. invasa* at three locations in Israel. Establishment of parasitoid populations was assessed between early March 2007 and early May 2008.

Location	Parasitoid spe- cies	Release		Recovery	
		Parasitoid liberation date	Number of released parasitoids	Total number of galls in the sample*	
Bet-Dagan	S. kryceri	20 Nov. 2007	~ 40	190	52
	Q. mendeli		~ 40		10
Segula	S. kryceri	25 Oct. 2007	42	210	10
	Q. mendeli		81		8
Nir David	S. kryceri	17 Sep. to 12 Nov. 2007	130	290	37
	Q. mendeli		550		18

^{*} From each gall 3–12 *L. invasa* may emerge

The percentages of parasitism inflicted by the two studied parasitoids, as related to the galling stage, are presented in Tables 1, 2. These percentages are relatively high (52 and 73% for *S. kryceri* and *Q. mendeli* respectively), considering the fact that the 10 female *L. invasa* and the two female wasps were allowed to oviposit for 24 h. In our tests females of *S. kryceri* and *Q. mendeli* successfully parasitized approximately 2.2 and 2.5 gall units per day, respectively.

A total of about 210 *S. kryceri* adults (~60% females), and about 670 *Q. mendeli* adults (all females), were liberated in three sites in the Coastal Plain and the Bet Shean Valley (Table 4). The first parasitoids were recovered 4 months after release. Galling material was sampled near the release spots in October 2007, and totals of 99 individuals of *S. kryceri* and 36 individuals of *Q. mendeli* were recovered from all three sites, suggesting that both species were acclimatized in Israel.

Discussion

Selitrichodes kryceri and Quadrastichus mendeli are larval parasitoids of L. invasa, although the possibility can not be excluded that both may also develop on related Leptocybe species that occur in Australia. At 25°C both parasitoids complete their development faster than a local Megastigmus sp. (Protasov et al. 2008) or an Australian Megastigmus sp. reared from L. invasa galls in Queensland: ~ 30 days vs ~ 40 days (study in progress). However, these eulophids develop more slowly and produce only about one-third as many offspring per day as compared with Closterocerus chamaeleon (Girault), the eulophid that was introduced to Israel to control another invasive gall wasp, Ophelimus maskelli. (Protasov et al. 2007a). C. chamaeleon also lives longer than S. kryceri and Q. mendeli (9 days vs 4 days, when fed on eucalyptus flowers). Thus, in light of the relatively small offspring production, the longer development and the shorter survival, it may be expected that the spread of S. kryceri and Q. mendeli for control of L. invasa will not be as swift and efficient as that of C. chamaeleon on O. maskelli.

The nutrition tests showed that adult *S. kryceri* and *Q. mendeli* displayed similar results to those of previously studied gall wasps and their parasitoids (Mendel *et al.* 2004; Huber *et al.* 2006; Protasov *et al.* 2007a, b, 2008). In all cases, host feeding was impossible, and females that were engaged in oviposition activity and were fed on honey solution lived for a shorter time than those that were supplied with honey solution and were not exposed to galls. All the studied wasps prolonged their survival by feeding on their host plant flowers. Millar *et al.* (2003) showed, with regard to two species of *Phoracantha* borers (Coleoptera; Cerambycidae), that eucalyptus flowers were better feed than other flowers for eucalyptus insects.

The studied parasitoids, *S. kryceri* and *Q. mendeli*, as well as their host, *L. invasa*, were found only in west central Queensland on young examples of the forest red gum tree, *E. tereticornis*. The fact that suitable galling material was found in young, fast-growing individuals is not surprising. Changes in tree age influence patterns of forest herbivory (Schowalter *et al.* 1986), and changes in herbivorous insect abundance on eucalyptus are known to coincide with phenological changes of their host plants (e.g., Abbott *et al.* 1992, 1999; Woinarski & Cullen 1984). Variations in leaf structural, chemical and nutritional properties may underlie associations with new or mature leaves and their susceptibility to galling (e.g., Ohmart & Edwards 1991), and in general most of the damage to tropical leaves occurs when they are young and expanding (e.g., Coley & Barone 1996). This behavior pattern suggests that *L. invasa* may be considered as an early colonizer of regenerated young stands in Australia. This may account for the efficient invasiveness of *L. invasa* in *Eucalyptus* plantations in four other continents, and may also imply that its parasitoids will display a similar fast tracking behavior in the new eucalyptus territories claimed by *L. invasa*.

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